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RITUALIZED AGGRESSION AND UNSTABLE DOMINANCE IN BROODS OF CRESTED IBIS (*NIPPONIA NIPPON*)

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ABSTRACT.—In broods of Crested Ibis (*Nipponia nippon*), aggressive dominance was unstable over time, even within feeding sessions. All chicks took turns pecking aggressively while broodmates hung their heads submissively, although roles were contested at the start of feeding bouts when chicks were 11–17 days old. In all broods, at least half of all pecks were *false pecks*, which did not strike broodmates even when within reach. False pecks seem to be ritualized displays that function to solicit food from parents and possibly to threaten rivals. *Received 9 July 2002, accepted 24 March 2004.*

We describe an extraordinary form of agonistic interaction between broodmates of the Crested Ibis (*Nipponia nippon*), a critically endangered ciconiiform (Liu 1981). Aggression among altricial broodmates occurs in a variety of avian taxa, including some ibises, egrets, raptors, boobies, anhingas, guillemots, and kingfishers (reviews in Mock 1984, Mock and Parker 1997, Drummond 2002). Generally, broodmate hierarchies are formed through pecking and biting (review in Drummond 1999), and, in species where siblicide is facultative (Lack 1947, 1954; Ricklefs 1965), the intensity of aggression varies with the amount of food provided by parents (Drummond 2001a, 2001b; but see Mock et al. 1987, Forbes and Mock 1994). Threatening postures and calls are common (Drummond 2001b), but no species has been reported to show ritualized attacks that do not impact the victim.

The Crested Ibis feeds on loaches, eels, locusts, and freshwater invertebrates, including insects, and lays two to four eggs in a tree nest; eggs hatch at 1- to 2-day intervals (Zheng 1973, Li and Huang 1986). Both parents feed the chicks by regurgitation until the chicks become independent at about age 70 days, 4 weeks after departure from the nest. Because of food competition, broods of most ibis species are facultatively reduced to two fledglings (Matheu and del Hoyo 1992), but brood reduction is relatively uncommon in Crested Ibis: 78.3% of hatchlings fledge (Zhai et al. 2001), compared to 56% ± 14.1 (SD) that fledge in 29 bird species with parental feeding and a modal clutch size greater than one (reviewed by Royle et al. 1999).

We recorded ibis behavior at hillside nests in Shaanxi Province (33° 18′ N to 33° 24′ N and 107° 23′ E to 107° 28′ E), China. Observers sat upslope of the colony at vantage points 15–50 m away from nests and watched broods through a telescope from 07:00–19:00 UTC + 08. Hatching order (a-chick, b-chick, and so on) was evident from marked differences in body size that persisted throughout the nestling period (as in the Bald Ibis, *Geronticus eremita*; Hirsch 1979). In 1999, we recorded behavior at nest 9918, where two broodmates, which hatched 2 days apart, were visible from a vantage point 30 m away. We observed behavior daily between hatching and fledging 41 days later, recording all feeding sessions on video. In addition, we observed seven broods of two, three, or four chicks (n = one, five, one broods, respectively) on 16 days (2.7 days/brood) in 1997, 1998, and 2000, when broods were in Stage 3 (>18 days old).

We recorded the absolute frequencies of *feeds* and *pecks*. During each parent's period of nest attendance, it typically fed the brood in a single session of two to eight regurgitations. Each regurgitation elicited a bout of chick aggression and a single feed. A feed was recorded whenever a chick received food by

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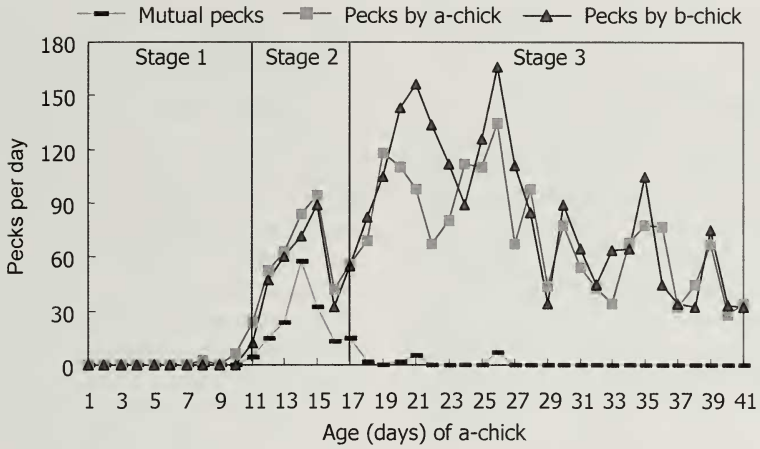

FIG. 1. Rate of pecking at a Crested Ibis (*Nipponia nippon*) nest, Shaanxi Province, China, 1999. The two chicks (brood 9918) pecked at similar rates, taking turns at aggressive pecking.

inserting its bill (usually its whole head) into the parent's bill. Pecks included any rapid downward thrust of the head, including *real pecks*, where open bill tips struck the broodmate (usually on the head or nape), and *false pecks*, where no target was struck and the downward thrust ended at the nest floor. The two categories of pecks were recorded simply as pecks because we often could not tell whether a peck was real or false. When the chicks at nest 9918 were aggressive during a bout (*mutual pecking*), they pecked at similar frequencies and it was difficult to count all pecks; thus, we counted only the mutual pecks of the more visible chick. Pecking frequencies of brood 9918 were recovered from video recordings, and those of the seven broods in Stage 3 were recorded using a hand counter. Video recordings were transferred from tape to Audio Video Interleave files using a VideoKing™ video compress card (Beijing Kefa Electronic Co. 1997), and those files were analyzed using Adobe Premiere 5.0 (Adobe Creative Team 1998).

Development of aggression and feeding.— In brood 9918, we categorized development of feeding and agonistic behavior into three stages, according to the age of the a-chick. During Stage 1 (0–10 days old), agonism was absent. During Stage 2 (11–17 days old), arrival of the parent at the nest was followed by a bout of begging and mutual pecking until one chick (a or b) submitted by hanging its head low, whereupon the other (aggressive) chick pecked for several seconds and the parent offered food to it. Sometimes, while the chicks were exchanging mutual pecks, the parent offered its open bill to one of them, which then fed. After submission by one chick, the other chick seemed to diminish its attacks. In Stage 3 (18–41 days old), upon arrival of the parent, one chick (a or b) started pecking and the other usually responded by hanging its head submissively. The aggressive chick then begged and was fed one or more times, all the while continuing to peck its unfed nestmate until the latter started to peck the aggressive chick and beg for food. Then the fed chick promptly hung its head submissively, and the unfed chick received the next feeding.

Chicks of brood 9918 begged, without vocalizing, by raising their bills and repeatedly tapping the parent's bill. Pecks at the broodmate usually were accompanied by simultaneous chirping, which occurred in no other context and was interpreted as a threat call. Aggression by both chicks of brood 9918 increased more or less steadily throughout Stage 2 and during the first 10 days of Stage 3, before declining steadily over the last 15 days of Stage 3 (Fig. 1). Parents provided 5.3 ± 0.8 (SD) feeding sessions per day, with 4.1 ± 2.1 regurgitations per session. Adults did not obviously interfere in broodmate aggression and tended to feed whichever chick was begging. Over the 41-day nestling period, the a-

chick received 483 feeds and the b-chick received 451 feeds.

In the other broods, all of the chicks showed aggressive pecking on every day of observation. This followed the pattern of brood 9918 in Stage 3, with chicks taking turns pecking and begging while their broodmates hung their heads submissively; there was no clear consistency with respect to which fed first or more frequently. Whenever a chick pecked, it pecked at all of its broodmates. There was no significant difference in the daily feeding frequencies of a-chicks and b-chicks (13.7 ± 4.7 and 12.3 ± 3.6 feeds, respectively; Wilcoxon rank sum test, $Z = 0.93$, $P = 0.35$, two tailed, $n = 7$) or of a-chicks, b-chicks, and c-chicks (12.3 ± 1.2, 12.1 ± 2.8, and 11.4 ± 3.3 feeds, respectively; Kruskal-Wallis test, $\chi^2 = 1.31$, $P = 0.52$, $n = 6$).

Dominance.—Dominance occurred when one chick was aggressive and the other adopted a submissive posture. Although a chick often dominated its broodmate briefly, dominance between chicks was unstable over time, even within feeding sessions. In brood 9918, over the 41-day nestling period, the a-chick pecked its broodmate 53.6 ± 39.4 times a day, versus 59.5 ± 48.5 pecks by the b-chick (excluding mutual pecking). In Stage 2, neither chick tended to dominate first and get the first feeding. Sometimes when the b-chick was pecking aggressively and about to be fed, the a-chick rose up and, using its superior height, intercepted the feed. In Stage 3, chicks were only fed while temporarily dominant, and similar feeding rates of the a-chick and the b-chick (XL unpubl. data) reflect similar frequencies of temporary dominance by the two broodmates. In most feeding sessions a single chick maintained dominance throughout, but successive dominance was also common. Thus, in Stage 3, 68% of the a-chick's 152 feeds were obtained in sessions where the a-chick dominated throughout or initially, and 32% in sessions where the b-chick dominated initially; for the b-chick's 171 feeds, the b-chick's corresponding values were 64 and 36%, respectively.

Similar absence of stable dominance appeared to be the rule in all dyads of the seven broods observed in Stage 3. For each brood we calculated the mean number of times each chick pecked its broodmates. The a-chicks and b-chicks (all broods) did not differ (86.8 ± 36.2 and 78.3 ± 31.4 pecks/day, respectively; Wilcoxon rank sum test, $Z = 0.886$, $P = 0.38$, two tailed $n = 7$). The a-chick, b-chick, and c-chick of each brood did not differ either (81.9 ± 25.0, 72.6 ± 21.5, and 73.1 ± 23.6 pecks/day, respectively; Kruskal-Wallis test, $\chi^2 = 2.02$, $P = 0.36$, $n = 6$).

False pecks.—False pecks included the threat call and frequently passed within centimeters of the broodmate, but they also occurred when the broodmate was out of range. Despite the victim being immediately in front, the aggressor directed pecks toward its own flanks, to one side and then the other, clearly avoiding the easy target (which might be standing with head lowered in submission) and striking nothing. False pecks occurred in all eight focal broods, and they appeared to represent roughly 60–70% of total pecks in brood 9918 and more than half of total pecks in each of the other seven broods. During mutual pecking, false pecks decreased to <10% of total pecks. False pecks occurred in Stages 2 and 3, usually after ordinary begging failed to elicit parental feeding. They could occur in the absence of genuine pecks at the broodmate, but they were almost invariably performed by the chick that currently dominated its broodmate. After fledglings departed the nest, real pecks were rare because victims promptly fled. False pecking continued during the next 4 weeks (when parental feeding was supplemented by attempts at self-feeding), even when the broodmate was out of sight. Like begging and real pecking, false pecking never occurred in the absence of a parent, and when false pecks occurred, parents offered food exclusively to the aggressor.

False pecking appears to be a ritualized form of real pecking, and both forms of pecking may elicit parental feeding. Originally, selection may have favored parents feeding aggressors, either because dominant chicks are more worthy of investment or because appeasing aggressors is a way of protecting their broodmates (when aggression is food dependent, Drummond 2001a). In either scenario, the door would be open for the evolution of signal function: parental feeding could be elicited initially by aggressive pecking and subsequently by false pecking. For the aggressor,

the advantage of using false pecks over real pecks may be that false pecks do less physical harm to the (long- and sensitive-billed) aggressor itself or to its sibling broodmate. Hence, false pecks could be more effective than ordinary begging for inducing regurgitation and ensuring feeding priority, and less costly than real pecks to the aggressor's individual and inclusive fitness.

Selection on parents to discriminate false pecks from real pecks would not necessarily result in parents declining to respond to false pecks. Discriminating parents could simply devalue the signal, responding to false pecks less than to real pecks (but more than to ordinary begging). Additionally, false pecking could be an especially potent signal if it also warns that violence will follow if food is not forthcoming or goes to the rival; it could deter rivals from begging, or blackmail parents into preferentially feeding the signaler. In brood 9918 at Stage 2, it seemed that whenever one chick begged during its broodmate's false pecking the broodmate responded by attacking more intensely, with real pecks.

False pecking may be associated with the Crested Ibis's unusual system of unstable broodmate dominance. Other aggressive brood reducers frequently attack even when food is not offered (Mock and Parker 1997), using real pecks to train broodmates into more permanent subordination (Drummond 2001b). For whatever reason, Crested Ibis chicks apparently attack only to secure immediate feeding priority, which may not require intense and extended violence.

Ultimately, false pecking may be related to the favorable ecological prospects of Crested Ibis broods, in which all young ordinarily fledge (Zhai et al. 2001). Because junior chicks do not usually face severe food shortage, they may pose only a negligible competitive threat to the survival of a-chicks, and as a consequence, a-chicks may be especially tolerant of them (Drummond et al. 2003). In Bald Ibis broods, however, frequent brood reduction signifies more severe food shortage (although chicks show successive dominance within feeding bouts, similar to the Crested Ibis); in this case, the order of dominance expression and access to food is dictated by a stable-dominance hierarchy and false pecking does not occur (Hirsch 1979, Oliver et al. 1979, Pegoraro and Thaler 1993, Tuckova 1999, Ros et al. 2001).

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LITERATURE CITED

Adobe Creative Team. 1998. Adobe Premiere 5.0: classroom in a book. Peachpit Press, Berkeley, California.

Bejing Kefa Electronic Co. 1997. Guide to VideoKing video compress card. Beijing Kefa Electronic Co. Beijing, China (in Chinese).

Drummond, H. 1999. Agonism and dominance in nestling birds. Proceedings of the International Ornithological Congress 22:1621–1631.

Drummond, H. 2001a. A revaluation of the role of food in broodmate aggression. Animal Behaviour 61:517–526.

Drummond, H. 2001b. The control and function of agonism in avian broodmates. Pages 261–301 *in* Advances in the study of behavior, vol. 30 (P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and T. J. Roper, Eds.). Academic Press, New York.

Drummond, H. 2002. Begging versus aggression in avian broodmate competition. Pages 337–360 *in* The evolution of begging: competition, cooperation and communication (J. Wright and M. L. Leonard, Eds.). Kluwer Academic Publishers, Dordrecht, The Netherlands.

Drummond, H., C. Rodríguez, A. Vallarino, C. Valderrábano, G. Rogel, and E. Tobón. 2003. Desperado siblings: uncontrollably aggressive junior chicks. Behavioral Ecology and Sociobiology 53:287–296.

Forbes, L. S. and D. W. Mock. 1994. Proximate and ultimate determinants of avian brood reduction. Pages 237–256 *in* Infanticide and parental care (S. Parmigiani and F. S. Vom Saal, Eds.). Harwood, Chur, Switzerland.

Hirsch, U. 1979. Studies of West Palearctic birds— 183 Bald Ibis. British Birds 72:313–325.

Lack, D. 1947. The significance of clutch size. Ibis 89:302–352.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon, Oxford, United Kingdom.

Li, F. L. and S. Q. Huang. 1986. The investigation of the reproduction behavior of the Crested Ibis. Bulletin of Biology 12:6–8 (in Chinese).

Liu, Y. Z. 1981. Rediscovery of the Crested Ibis in Q Mountain. Acta Zoologica Sinica 27:273 (in Chinese).

Matheu, E. and J. del Hoyo. 1992. Family Threskiornithidae. Pages 472–506 *in* Handbook of the birds of the world, vol. 1: ostrich to ducks (J. del Hoyo, A. Elliott, and J. Sargatal, Eds.). Lynx Edicions, Barcelona, Spain.

Mock, D. W. 1984. Infanticide, siblicide, and avian nestling mortality. Pages 3–30 *in* Infanticide: comparative and evolutionary perspectives (G. Hausfater and S. B. Hrdy, Eds.). Aldine, New York.

Mock, D. W., T. C. Lamey, C. F. Willliams, and B. J. Ploger. 1987. Proximate and ultimate roles of food amount in regulating egret sibling aggression. Ecology 68:1760–1772.

Mock, D. W. and G. A. Parker. 1997. The evolution of sibling rivalry. Oxford University Press, Oxford, United Kingdom.

Oliver, W. L. R., M. M. Mallet, D. R. Singleton, and J. S. Ellett. 1979. Observations on the reproductive behavior of a captive colony of Bare-faced Ibis *Geronticus eremita*. Journal of the Jersey Wildlife Preservation Trust 16:11–35.

Pegoraro, K. and E. Thaler. 1993. Postembryonic development and juvenile phase of the Northern Bald Ibis or Waldrapp Ibis *Geronticus eremita*. Okologie der Vogel 15:155–192 (in German).

Ricklefs, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67:505–510.

Ros, A. F. H., K. Hirschenhauser, and R. F. Oliveira. 2001. The interaction between organizational and activational effects of testosterone in the control of early aggression in birds: a comment on Sasvári, Hegyi and Péczely. Ethology 107:851–853.

Royle, N. J., I. R. Hartley, I. P. F. Owens, and G. A. Parker. 1999. Sibling competition and evolution of growth rates in birds. Proceedings of the Royal Society of London, Series B 266:923–932.

Tuckova, K. 1999. Nestlingsaggression bei Waldrappen (*Geronticus eremita*). M.Sc. thesis, University of Vienna, Austria.

Zhai, T. Q., X. R. Lu, B. Z. Lu, Y. M. Zhang, and H. J. Wang. 2001. Nest building, egg laying, hatching, and breeding of Crested Ibis (*Nipponia nippon*). Acta Zoologica Sinica 47:508–511 (in Chinese).

Zheng, Z. X. 1973. The avifauna of Qinling Mount. Chinese Science Press, Beijing, China (in Chinese).